MADROÑO, Vol. 61, No. 1, pp. 115–125, 2014

RELATIONSHIPS BETWEEN EPIDERMAL BROWNING, GIRDLING, DAMAGE, AND BIRD CAVITIES IN A MILITARY RESTRICTED DATABASE OF 12,000+ PLANTS OF THE KEYSTONE *CARNEGIEA GIGANTEA* IN THE NORTHERN SONORAN DESERT

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ABSTRACT

An exceptional dataset for over 12,000 *Carnegiea gigantea* collected by the Arizona Department of Game and Fish over two field seasons on a restricted military reservation was released to the authors for analysis, including a variety of variables for which little empirical evidence exists. Data on epidermal browning, physical damage due to fire, lightning, gunshot or topping, rodent girdling, bird cavities and other variables were assessed using primarily chi-square analysis. The main findings of this study include: (1) Plants with high amounts of epidermal browning were rather evenly distributed across height classes, although the very smallest plants (0–0.9 m) had substantially less epidermal browning. (2) Although past work has shown that epidermal browning is surely a function of solar radiation receipt, other variables (bird cavities, girdling, damage, branching) are statistically linked with browning, raising the possibility that other biotic and abiotic factors may hasten browning. (3) Bird cavities are better predicted by height than branches, likely due to decreased visibility and exposure to thermally tempering winds caused by branches, and improved defensive position and reduced exposure to heating from the surface associated with taller plants.

Key Words: Bird cavities, epidermal browning, *Larrea tridentata*, lightning, nurse plants, saguaro cactus, Sonoran Desert.

Carnegiea gigantea (Engelm.) Britton & Rose (saguaro, Cactaceae) is a columnar cactus that may reach 10 m or more in height, and is a keystone species (Fleming 2002) upon which nearly every animal species in the Sonoran Desert ecosystem relies on wholly or in part for their survival. While nurse-associations and relationships between *C. gigantea* and a variety of key climate variables have been well studied (Niering et al. 1963; Steenbergh and Lowe 1983; Drezner 2004a, b; Drezner and Balling 2008), many more localized influences are less widely understood, often due to limitations in data. Some of these variables include the impacts of girdling and natural and anthropogenic causes of damage, as well as the linkages between these, epidermal browning, and bird cavities over large populations.

Girdling, where animals consume the outer fleshy portions of the cactus, often but not exclusively near the base (within reach of the animal), has been observed (Steenbergh and Lowe 1983). Few animals (e.g., the woodrat *Neotoma albigula* [Hartley 1894]) rely on the flesh of *Carnegiea* Britton & Rose due to the presence of oxalates, though a variety of species may consume some of the plant under conditions of stress (Schmidt-Nielson 1964; Steenbergh and Lowe 1977). Steenbergh and Lowe (1983) note that girdling is not fatal, but may hasten death through other causes, such as windthrow or freezing mortality. Little else has been published on the effect of girdling in *Carnegiea*. Human impacts have been considered indirectly through invasive species (Schiermeier 2005; Stevens and Falk 2009) and livestock grazing (Niering et al. 1963; Niering and Whittaker 1965; Abou-Haidar 1989). Direct human impacts on individual plants, such as bullet holes or other damage, have not been well studied, nor have other types of damage that occur naturally (e.g., decapitation, damage from proximate trees).

Many species of birds create cavities in plants while others use pre-existing cavities (e.g., Kerpez and Smith 1990a). Many studies have looked at nest orientation and other bird preferences and patterns (Inouye et al. 1981; Goad and Mannan 1987; Kerpez and Smith 1990b), but far less work has been done on the impact of such cavities on the *Carnegiea* plant itself. Steenbergh and Lowe (1983) note that some large, mature, branched plants can support dozens of bird cavities and only occasional decapitation is associated with these nest cavities. Such decapitation results from vulnerability to freezing in those locations on the plant (Steenbergh and Lowe 1983).

Epidermal browning is where epicuticular waxes accumulate and sheeting occurs obscuring stomata, causing scaling, barking and browning of the parenchyma (Evans et al. 1994a). Epidermal browning occurs overwhelmingly on the sun-facing side of the plant (Evans et al. 1992) over large geographic areas in both hemispheres (Evans et al. 1992; Evans et al. 1994b), leading researchers to suggest that solar radiation contributes to epidermal browning (Evans et al. 2001). Extensive epidermal browning has been associated with an annual mortality rate of 2.3% in a population of this long-lived species (Evans et al. 2005).

A *Carnegiea gigantea* inventory was carried out at the Florence Military Reservation, an active military training area that is closed to the public, in order to assess the natural resources on the installation. This effort yielded a wealth of data for over 12,000 *Carnegiea gigantea* plants (plus their nurse plants), over an area of over 11 km^2. Except for a single study constructing the age structure of those plants based on their height (Danzer and Drezner 2010), we analyze that dataset here. The data are owned by the Arizona Army National Guard and the authors have been granted permission to analyze and publish the findings from the dataset. This includes several variables that are not well studied in the species, and this database provides an exceptional opportunity to assess them.

The very rich dataset for this military base includes data for all of these variables (epidermal browning, girdling, damage, bird cavities) as well as others as described below, and provides a rare opportunity to analyze variables that are currently poorly understood, as well as to confirm better studied variables with a large dataset. Some of these variables and factors are very common, yet surprisingly unknown, despite the keystone status of the species. Understanding these common ecological elements is important for understanding the sustainability of the species and the environmental controls and human impacts on the species. This is the first study to investigate many of these relationships.

Methods

Study Site

The Florence Military Reservation (Fig. 1) is home to a variety of species, including the keystone *Carnegiea gigantea* (Fleming 2002) as well as the keystone *Olneya tesota* A. Gray (Fabaceae). Other common species include *Larrea tridentata* (Sessé & Moc. ex DC.) Coville (Zygophyllaceae), *Encelia farinosa* A. Gray ex Torr. (Asteraceae), *Fouquieria splendens* Engelm. (Fouquieriaceae), *Cercidium* Tul. spp. (Fabaceae), *Prosopis* L. spp. (Fabaceae), and *Opuntia* Mill. spp. (Cactaceae). The area sampled in this study is 11.07 km^2 in size and access is restricted to military personnel. This executive order land is federal land that is owned by the military that was given to the Arizona National Guard in 1912, though it is not state property.

Rain falls in two distinct seasons in the Sonoran Desert. Summer storms form convectively with the Arizona monsoon (Carleton 1986, 1987), while extra tropical mid-latitude cyclones bring cold season rainfall to the region (Sheppard et al. 2002). The Florence, Arizona meteorological station is about four km from the study area (station #023027 at 33°02′N, 111°23′W). Data from this meteorological station from 1892–2009 show that mean annual precipitation is 252.5 mm. July precipitation averages 32.0 mm, and January precipitation averages 25.4 mm. Summers are hot, with daytime high temperatures in July averaging 40.8°C, and daytime high temperatures averaging 19.1°C in January.

Field Methods

The *Carnegiea gigantea* inventory was carried out by the Arizona Department of Game and Fish (AZGF) in Spring 2006 and Spring 2007. These personnel are biologists engaged in a variety of monitoring projects throughout the state and for other agencies, and have often extensive field experience. The data are owned by the Arizona Army National Guard and the authors have been granted permission to use the dataset. Field personnel systematically walked 50 m wide belt transects to collect data, as well as collecting Universal Transverse Mercator (UTM) coordinates for each *C. gigantea* encountered that was at least 10 cm tall. Only living plants were included.

For each *Carnegiea* sampled, a variety of data were collected. The height of the plant to the nearest 10 cm was measured using a hypsometer for plants greater than two m in height, and a measuring pole for the smaller plants. Number of primary branches (off the main stem), secondary (growing from a primary branch), and tertiary (growing from a secondary branch) branches (defined by being at least the size of a golf ball) were counted for each cactus. Presence of a nurse plant was determined, and the species noted. This was specifically targeted towards *Carnegiea* up to one m in height. Epidermal browning was logged for each plant (%Green) based on the amount of the plant's epidermis that was green and thus photosynthetically active as follows: less than 50% green (category 1), 50–75% green (category 2), 75–99% green (category 3), and plants that were 100% green (category 4). For each plant, areas with black or brown discoloration, and/or

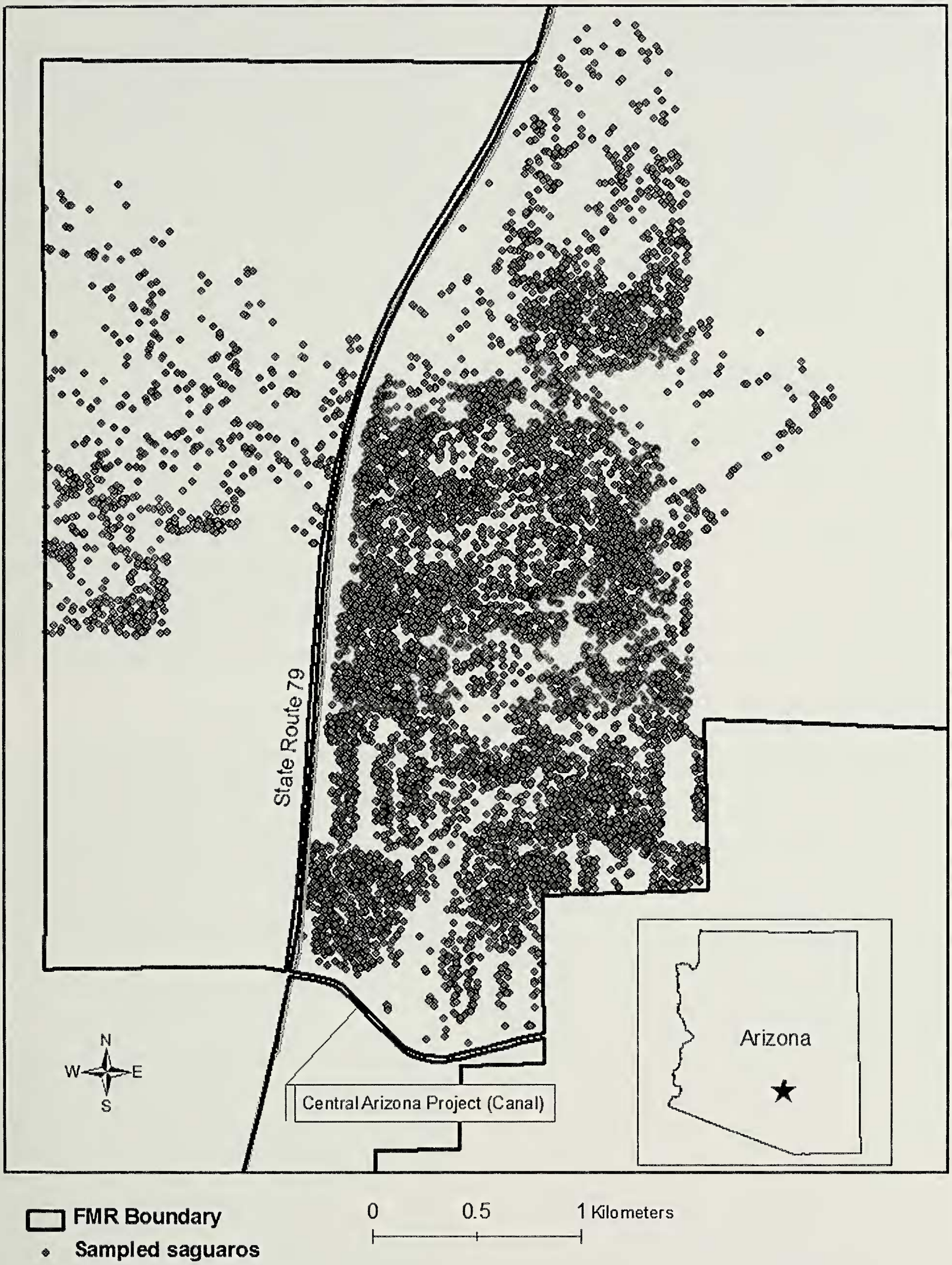

FIG. 1. Map of the study site showing the location of the sampled plants at the Florence Military Reservation (Florence) in Arizona.

that appear to be scabby or corky, or appear to have a bark-like surface were noted, and epidermal browning was visually assessed for each plant in the field during data collection using the %Green classes. Presence/absence identifications were made for evidence of trunk girdling by rodents. Natural and anthropogenic damage was documented for a variety of categories including fire, lightning, gunshot, and topping, which refers to the decapitation or absence of the upper portion of the main stem. For each plant, the number of bird cavities at least five cm in diameter and "deep enough so that the back of the cavity cannot be seen" was recorded.

Statistical Methods

The database included a variety of variables for each *Carnegiea* sampled, including plant height (cm), and numbers of primary, secondary, and tertiary branches. We generated the additional variable of *total number of branches*, representing the sum of these three. Nurse species data were primarily for the smallest individuals, as noted above in the Field Methods section, but some identifications had also been made for larger plants. Other variables included %Green (4 ordinal classes of epidermal browning), presence/absence of trunk girdling, damage classifications (analyzed as a group and also by individual classifications), and number of bird cavities on each plant. Analyses were conducted using the chi-square test of independence as the dataset is made up primarily of classes and frequency data and few if any variables are normally distributed or can be transformed to approximate a normal distribution.

To assess the seven variables (height, total number of branches, nurse species, %Green, girdling, damage, number of bird cavities), we used chi-square tests of independence. Chi-square tests were run on all pairs of variables (e.g., %Green and girdling, %Green and damage, etc.), except for several analyses that were limited to taller plants (e.g., involving branches, bird cavities). The variable 'nurse species' only included the more common species (*Larrea tridentata, Cercidium microphyllum* (Torr.) Rose & I. M. Johnst., and *Olneya tesota*). *Ambrosia deltoidea* (Torr.) W.W. Payne was excluded from the nurse species groupings as it has been well established that with their relatively short life span, individuals often establish in proximity to a *Carnegiea* after the cactus has already established, and thus that *Ambrosia* L. is not the nurse (Hutto et al. 1986). Also, damage identification was limited to clear identifications (e.g., the "unknown" category in the database was excluded). Because multiple tests are run on the dataset, the sequential Bonferroni test is applied to correct for type-I errors associated with repeated testing of the same dataset (Rice 1989).

Because many of these variables may also be impacted by height (e.g., girdling might increase with height [age]), a second round of analyses was conducted (with the sequential Bonferroni correction) just for plants between 4–6 m in height to control for any such effects, except for pairings involving height or nurse species. Due to the high frequency of identifications for smaller *Carnegiea*, the analyses for nurse species were done instead for plants 1–1.9 m in height only (instead of 4–6 m). In some of the analyses (both for the original tests described above and the height-controlled tests), categories had to be merged due to small expected values in the chi-square tests (e.g., %Green categories 1 and 2).

Two Pearson product-moment correlation analyses were done between bird cavities and number of branches and height to establish whether bird cavities are better predicted by *Carnegiea* height or number of branches for plants two m in height and taller. That is, are there more bird cavities because a plant is tall, or because there is more available space to establish within the many branches? Correlation is also used to ascertain the relationship between *Carnegiea* height and presence of primary, secondary, tertiary, and total number of branches.

Results

A second dataset of the dead plants at the site listed 1103 dead individuals. If combined, (12,238 living +1103 dead), 8.3% of the plants were dead. We did not utilize this secondary, dead plant dataset in this study. The remainder of this manuscript refers to analyses conducted on the main 'living' dataset of 12,238 plants. The sequential Bonferroni test confirms the significance of all chi-square tests ($P < 0.05$).

Epidermal Browning

Presence of bird cavities is not independent of %Green ($P = 8.8 \times 10^{-69}$, $n = 5085$ for plants three m and taller in height, Table 1), where a higher than expected frequency of plants are observed in categories 1 and 2 in %Green that have bird cavities. The statistical significance is confirmed for the 4–5.9 m height range ($P = 5.2 \times 10^{-10}$, $n = 2605$). Epidermal browning is also related to girdling, where lower girdling frequencies are observed in plants with %Green ratings of 4 (for the full dataset ($P < 1.0 \times 10^{-300}$, $n = 12{,}177$, Table 1) and when controlling for height ($P = 1.6 \times 10^{-5}$, $n = 2597$). Epidermal browning is also related to damage, where lower damage frequencies occur in the higher %Green classes ($P = 3.6 \times 10^{-229}$, $n = 11{,}294$), confirmed in the 4.0–5.9 height class only to control for the influence

TABLE 1. SELECTED FREQUENCIES AND CHI-SQUARE TESTS AND RESULTS. Abbreviations include girdling (Gird), absent (A), present (P), damage (Dam), number of bird cavities (Bird), and %Green classifications for epidermal browning (1: <50% green; 2: 50–75% green; 3: 75–99%; 4: 100% green, i.e., no epidermal browning). Also provided are the p-value results for the chi-square test of independence (0 represents a value smaller than 1.0×10^{-300}), the sample size (n), and additional notes.

	%Green 1	%Green 2	%Green 3	%Green 4	p-value	n	Notes
Gird A	73	285	3182	3150	0	12,177	
Gird P	121	684	4465	217			
Dam A	87	489	6037	3340	3.6×10^{-229}	11,294	
Dam P	78	275	969	19			
Bird 0	88	541	3674	168	8.8×10^{-69}	5085	≥3 m in height only
Bird 1+	53	209	344	8			

of height ($P = 7.2 \times 10^{-13}$, $n = 2300$). For %Green and total number of branches, greater branching tended to show lower frequencies in the higher %Green categories ($P < 1.0 \times 10^{-300}$, $n = 12{,}202$), and the results remain significant when isolating only plants 4–5.9 m in height ($P = 0.03$, $n = 2605$).

By height, %Green had an unusual (and significant) pattern. The two higher classes %Green 3 and 4, clearly had greater frequencies of plants at lower heights (i.e., browning increases with height), but in the low %Green categories 1 and 2, the distribution was more even and any trends were less apparent (Fig. 2).

Girdling

Girdling is not independent of epidermal browning (as described above). Girdling and damage are not independent, as there is more girdling on damaged plants and non-girdled plants have a relatively lower frequency of damage ($P = 1.4 \times 10^{-84}$, $n = 11{,}297$; height controlled: $P = 0.00012$, $n = 2301$). Girdling increases with height, but girdling is independent of nurse species, total number of branches and bird cavities. As observed below, topping may be linked to girdling.

Damage

As noted above, %Green and girdling are statistically related to damage. Not surprisingly, damage increases with plant height, as well as with bird cavities (which are not a component of damage) (damage and bird cavities: $P = 2.2 \times 10^{-58}$, $n = 11{,}328$; height controlled: $P = 1.4 \times 10^{-6}$, $n = 2309$). Damage is independent of total number of branches when height is controlled for (in the 4–5.9 m tall subset).

A total of 114 plants were identified as having some sort of fire damage and 345 plants as having gun damage. Seven plants were identified as having lightning damage, while nearly 10,000 of the plants were identified as having no damage. Further, 257 plants were identified as being topped (that is, the top portion of the main stem was absent). Of these, 178 were identified as being 75–100% green, and 22 had no bird cavities. Seventy-five percent (191/254) however, were identified as being girdled. By comparison 5504/12,205 (45%) plants were girdled in the entire dataset. Some types of damage are provided in Table 2.

Bird Cavities

In addition to the relationships outlined above, bird cavities and nurse species is marginally insignificant ($P = 0.053$, $n = 1931$), though it should be noted that sample sizes are small as cacti with sampled nurses are primarily the smallest plants, while birds tend to establish on taller plants. In the control subset of plants 1–1.9 m in height, only one bird cavity was recorded among the three main nurse species.

Chi-square results show that plant height ($P = 1.6 \times 10^{-212}$, $n = 6042$ for plants 2 m and taller) and number of branches (height-controlled: $P = 7.1 \times 10^{-10}$, $n = 2614$) are both significantly related to bird cavities. Correlation results to determine which of these two variables (plant height or number of branches) is the better predictor of bird cavities, particularly considering the very strong relationship between plant height and branching, show that plant height is a superior predictor of cavities ($P = 5.7 \times 10^{-157}$, $n = 6042$) than number of branches is in predicting cavities ($P = 2.2 \times 10^{-95}$, $n = 6042$). Interestingly, total number of branches had a stronger relationship with bird cavities ($P = 2.2 \times 10^{-95}$) than number of primary branches ($P = 7.0 \times 10^{-82}$, $n = 6042$), and secondary ($P = 3.8 \times 10^{-35}$, $n = 6042$) (and tertiary) branches had weaker correlations still, though all were significant, likely due in part to the large sample size.

Branches, Nurse Plants, and Height

The distribution of branches on *Carnegiea* by height is shown in Fig. 3. The strongest correla-

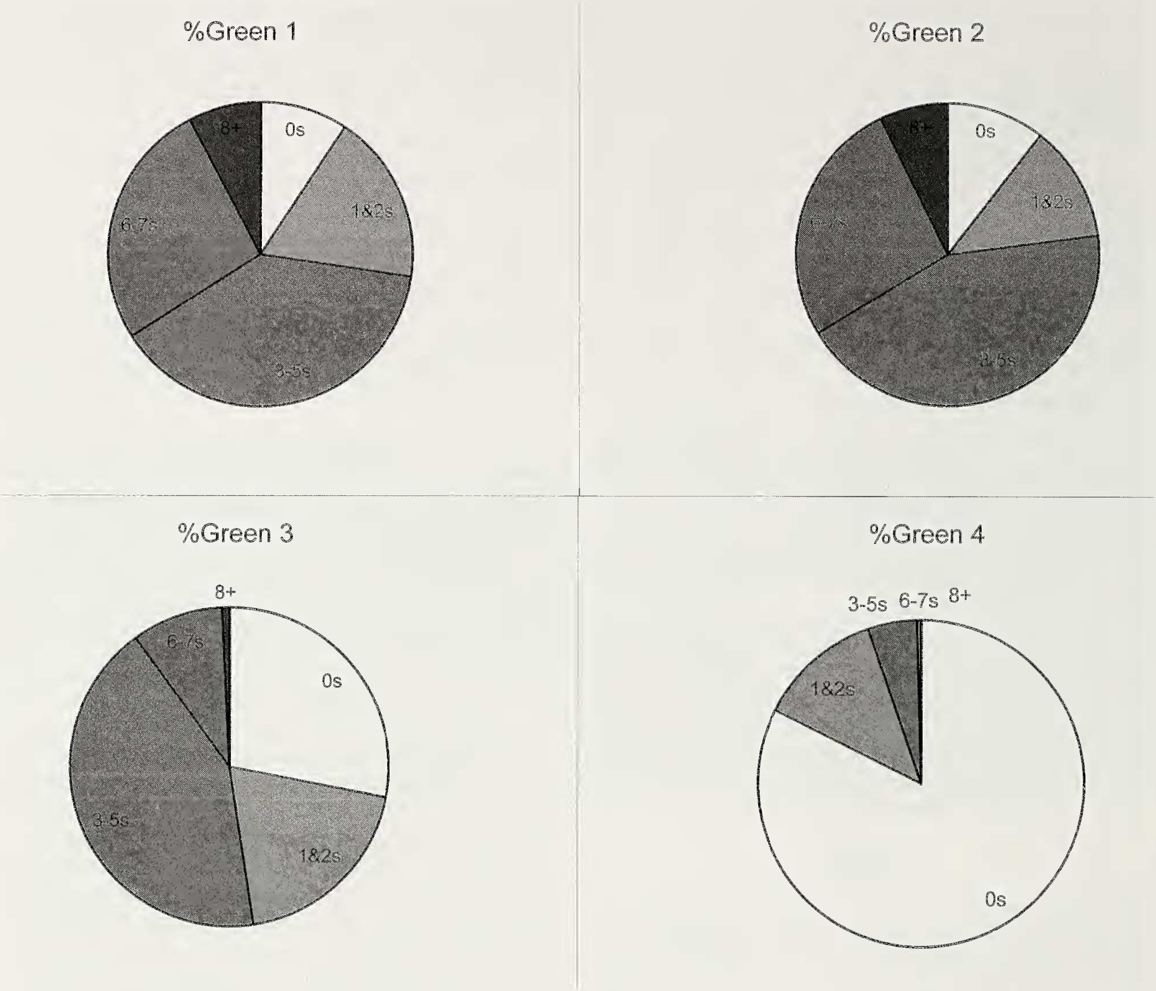

FIG. 2. *Carnegiea* plant frequencies by different height classes in each epidermal browning class. %Green represents the amount of the plant that does NOT have epidermal browning and classifications are: %Green 1: <50% green; %Green 2: 50–75% green; %Green 3: 75–99%; %Green 4: 100% green. Height classes are 0: plants 0–0.9 m in height; 1: 1.0–1.9 m; 2: 2.0–2.9 m, etc. to 8+ which includes all plants 8.0 m in height and taller. For these charts, some classes were merged for ease of interpretation. For example, most plants with no epidermal browning (%Green 4) are 0–0.9 m in height.

tion is between height and number of primary branches ($P < 1.0 \times 10^{-300}$, $n = 6042$, $F = 2580.8$), followed by height and total number of branches ($P < 1.0 \times 10^{-300}$, $n = 6042$, $F = 2327.7$), with secondary ($P = 5.2 \times 10^{-11}$, $n = 6042$) branches (only 14 plants have tertiary branches) exhibiting a weaker relationship with height.

TABLE 2. FREQUENCIES OF VARIOUS CLASSIFICATIONS OF DAMAGE (FIRE, GUN, LIGHTNING, TOPPED (DECAPITATED), TREE, AND NO DAMAGE [NONE]) AND OTHER VARIABLES INCLUDING GIRDLING (ABSENT, PRESENT) AND EPIDERMAL BROWNING %GREEN CATEGORIES (1: <50% GREEN; 2: 50–75% GREEN; 3: 75–99%; 4: 100% GREEN, I.E., NO EPIDERMAL BROWNING).

	Girdling		Epidermal browning			
	A	P	%Green 1	%Green 2	%Green 3	%Green 4
Fire	66	44	35	44	31	0
Gun	118	214	9	96	221	6
Lightning	0	7	0	4	3	0
Topped	63	191	20	59	175	3
Tree	185	450	14	71	539	10
None	6009	3949	87	489	6037	3340

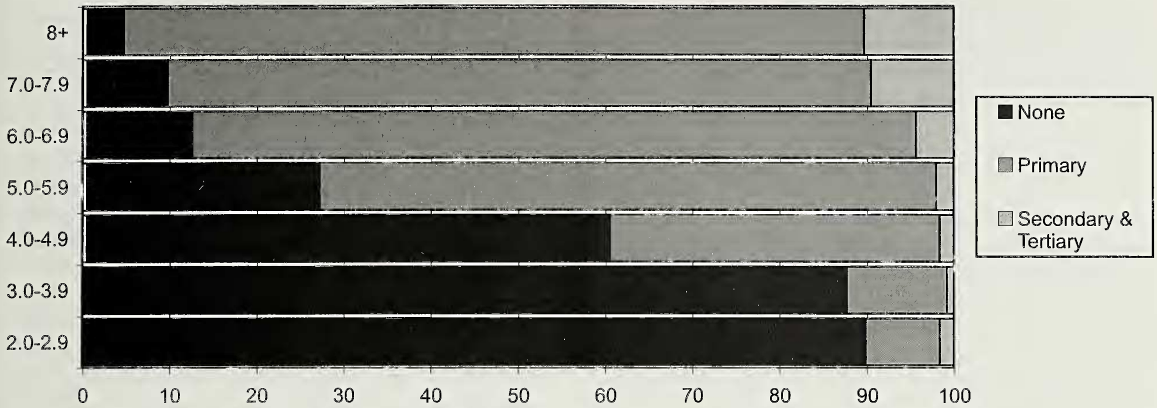

FIG. 3. Distribution of branches by height starting at two m. None represents plants with no branches. Primary represents the frequency of plants (not number of branches) that have only primary branches (those emanating from the main stem). Secondary and Tertiary represents the number of plants that have at least one branch emanating off of a branch. Each height bar is scaled to 100% of plants in that height class, so the branch classes are depicted as a proportion rather than raw frequency. The height classes are in meters (e.g., the shortest class includes plants between 2.0–2.9 m in height). 8+ includes all plants 8.0 m in height and taller.

Finally, there were 5220 plants between 0–1.0 m in height. Of these, 50.3% are nursed by *Ambrosia deltoidea*, 17.7% by *Larrea tridentata*, and 10.8% *Cercidium microphyllum*. A wide variety of other species make up the remainder of the nurse identifications.

Discussion

Epidermal Browning

Epidermal browning is associated with scaling and barking as well as loss of spines (Evans et al. 1992) on a variety of columnar cactus species (Evans and Fehling 1994; Evans et al. 1994b). It is far more common on the south-facing side of *Carnegiea* plants (Evans et al. 1992), and in South American cacti, epidermal browning is predominantly on the northern equator-facing sides of plants (Evans et al. 1994b) and browning is lessened on those plants shaded on their sun-facing side by larger nurse plants (Evans et al. 1994a). The pattern is widespread over large intra-continental areas (Evans et al. 1992). Epidermal browning is not related to trace metal pollution (Kolberg and Lajtha 1997). Mounting evidence has linked browning to solar radiation (Evans et al. 2001), and they suggest more specifically that UV-B radiation causes browning, though other work does not confirm this (Lajtha et al. 1997). At Saguaro National Park, epidermal browning has been linked with premature death of these cacti (Evans et al. 2005). Other factors that may contribute to epidermal browning should be considered, such as tissue heating (Drezner 2011) above lethal temperatures (McAuliffe 1996). Regardless, epidermal browning may predict future longevity of plants and may result in premature mortality (Evans et al. 2005). Epidermal browning is found across numerous taxa, including across many genera of columnar cacti throughout the Americas (Evans and Fehling 1994; Evans et al. 1994b; Evans 2005) as well as several succulent South African *Euphorbia* species (Evans and Abela 2011).

The association between height and browning has been recognized (Duriscoe and Graban 1992), where browning increases with *Carnegiea* height. Of plants with greater epidermal browning (categories 1 and 2 of %Green), the frequencies are rather evenly distributed (fluctuating from 5–15% in category 1 plants across the one meter height classes to nine meters, and for category 2, from 5–18%). That is, plants with greater epidermal browning are fairly evenly distributed across the height spectrum. Conversely, of individuals with little to no browning, the 0–0.9 m height class has 28% of all category 3 %Green individuals, and 82% of all category 4 individuals. Thus, individuals that have little epidermal browning are dominantly smaller plants, but plants with high amounts of epidermal browning span the entire height range relatively evenly.

There were significantly more bird cavities associated with plants with a lower %Green classification (height-controlled). Whether this is due to avian preferences for plants, for example, with fewer spines (associated with epidermal browning), or whether bird cavities may act to hasten browning is uncertain. Plants with greater girdling also appear to be less green, particularly apparent in the significantly low frequency of plants that are in the highest %Green class and also girdled. Plants without recorded natural and anthropogenic damage are more frequent in the higher %Green classes. Even branching appears to be related to %Green, where browning increases with branches. While solar radiation is surely the primary cause of epidermal browning, perhaps these other factors weaken the plant or hasten the browning process.

Girdling

Greater girdling is observed on damaged plants (damages not associated with rodent action). It is notable that girdling increases with height. Taller plants may be more girdled simply due to greater time periods over which there was opportunity for small mammals to cause the girdling. It is also possible that several variables are confounded, particularly in relation to height. Spine loss increases with epidermal browning and thus presumably with height (Duriscoe and Graban 1992), which may increase the attractiveness of taller plants to small mammals for girdling. Epidermal browning is related to girdling; whether this relationship is direct (girdling hastens browning or browning draws rodents for girdling), or confounded by another variable confounded by height is uncertain though plants with no epidermal browning are disproportionately ungirdled while girdled plants are underrepresented in the highest percent green class. This supports past observations that epidermal browning may hasten death and provides some indication of the overall health of the plant (Evans et al. 2003; 2005). It is possible that epidermal browning may be hastened by damage. Also, as *Carnegiea* plants get taller, they generally get thicker (Drezner 2003a), so greater available plant material may draw rodents, increasing girdling on taller plants. However, the chi-square results for the height-controlled subset of the sample maintain the significant relationship between girdling and epidermal browning (%Green) and the relationship between girdling and damage (though bird cavities are independent of girdling). Perhaps plants are weakened by girdling making them more prone to at least some types of damage (Steenbergh and Lowe 1977, 1983); damage classifications were primarily tree, topped, gun, and fire. The data (Table 2) show that while fire frequency data are similarly distributed to the no damage data, girdling is disproportionately more common for topping, tree and gun damage. Damaged plants may also be compromised making them more attractive to rodents for girdling. Also, small mammals may seek out plants with greater epidermal browning and spine loss. Rogers (1985) suggests that *Carnegiea* individuals with spine loss may be at greater risk of contact with cattle.

Despite the possibility that girdling may hasten mortality by increasing susceptibility to windthrow and freezing, this is relatively rare (Steenbergh and Lowe 1977, 1983). Nurse species, and thus architecture (trees versus the open *Larrea* shrub nurse), is also independent of rodent girdling of cacti.

Damage

Since plants get taller with age, it is not surprising that damage increases with height, as there is more time over which damage can occur. In fact, the damage classifications are inherently height related. Potential damage from a tree or topping increase with height, as does the likelihood of being struck by lightning as the tallest individuals are disproportionately struck (Steenbergh 1972), or being used as a target for gunfire. Estimates suggest that lightning kills, "much less than 0.1% of the population per year" (Steenbergh 1972; Steenbergh and Lowe 1983, pp. 137). Our dataset has only seven lightning strike identifications that represent 0.06% of the plants in total, in strong agreement with past observations (Steenbergh 1972). Our value is not adjusted per year, however Steenbergh (1972) suggests decomposition is rapid in such cases. Decapitation was documented in 2% of the sample. Of those 2%, nearly 70% had less than 25% epidermal browning. Girdling, however, was documented in 75% of decapitated plants, compared to the dataset average of 45% girdled plants.

Damage increases with bird cavities (also when controlling for height). In the northern Sonoran Desert, *Carnegiea* decapitation (=topping) may occur where freezing occurred at a bird cavity (Steenbergh and Lowe 1977). Bird cavities thus increase a plant's susceptibility to topping (Steenbergh and Lowe 1983; McAuliffe and Hendricks 1988), but other damage types are less clear in their possible association with bird cavities. For example, perhaps some gunfire targets birds rather than the plants, or that birds may utilize bullet entry points for nest excavation. When isolating plants that are 5.0–6.9 m in height only, the observed number of plants with bird cavities and with gun damage (versus no damage) is significantly higher than expected (data not shown). The impact of bird cavities naturally on *Carnegiea gigantea* populations is relatively small (Steenbergh and Lowe 1983). Branches however, is independent of damage.

The presence of combustible material or a substantial ground covering of grass or other vegetation that encourages fire burn and spread is strongly related to *Carnegiea gigantea* fire damage and mortality, while *Carnegiea* in more barren or rocky areas appear to suffer far less (Steenbergh and Lowe 1977). Mortality may exceed 70% in burned areas (Rogers 1985). Smaller plants are particularly susceptible and may be underrepresented in estimates (Rogers 1985). Our dataset shows 110 plants (Table 2) with fire damage, representing less than 1% of the population. Not surprisingly, buffelgrass (*Pennisetum ciliare* (L.) Link), a major contributor to combustible ground cover and fire damage in the Sonoran Desert [Schiermeier 2005]) is not well established at this site. Ground cover at this site is rather sparse except during unusually wet winters when a generous cover of annuals becomes established. However, as an active military training site, the potential for ignition is ever present.

Bird Cavities

Bird cavities are significantly related to both plant height and to total number of branches (which are themselves strongly related [Drezner 2003b]). Korol and Hutto (1984) found a positive association between bird cavities and branching, and large, old, often heavily branched *Carnegiea* may support 50 woodpecker cavities (Steenbergh and Lowe 1983). Correlation indicates that total number of branches is a stronger predictor of bird cavities than number of primary branches, further supporting the overall importance of branches for presence of avian nesting cavities. However, our correlation results show that number of bird cavities is better predicted by plant height than by number of branches. While branching increases available 'real estate' for bird cavities (and is a significant predictor), height appears to be the superior predictor. On the highly branched *Pachycereus pringlei* (S. Watson) Britton & Rose (cardon), bird cavities are oriented in directions with fewer branches in order to maximize visibility (Zwartjes and Nordell 1998), leading to the possibility that branches, or excessive branching, may result in some bird avoidance of such highly branched cacti. Further, branches act as a windbreak, which is detrimental for some species such as the Gilded Flicker (*Colaptes chrysoides* [Malherbe 1852]); they excavate nesting sites that face into the prevailing wind direction as this aids in cooling (Zwartjes and Nordell 1998). Gila woodpeckers (*Melanerpes uropygialis* [Baird 1854]) show a preference for cavities that are higher above the ground which may be related to greater predation risk near the ground, difficulties associated with excavating smaller plants, or even greater thermal stress in nests in cavities that are closer to the ground (Korol and Hutto 1984). It is also possible, however, that there is greater opportunity for bird cavities to accumulate in taller plants (McAuliffe and Hendricks 1988).

The relationship between bird cavities and nurse species, although marginally insignificant, is decidedly inconclusive as the vast majority of bird cavities are in taller plants, while nurse species were recorded primarily for shorter plants. In the 1.0–1.9 meter height-controlled subset, only one bird cavity was recorded across the three nurse species analyzed in this study (of $n = 236$ *Carnegiea* associated with these nurse plants).

Conclusions

Our study sheds light on many previously unknown factors related to the Sonoran Desert keystone species, *Carnegiea gigantea* and its ecology, including: (1) Plants with large amounts of epidermal browning are evenly represented across height classes, fluctuating from about 5–15% up to plants nine meters in height. However, plants with little to no sign of epidermal browning have very high representation in the smallest height class (0–0.9 m). (2) Epidermal browning is associated with the presence of bird cavities, girdling, natural and anthropogenic damage, and branching. Whether these individually hasten browning or are the result of it (for example perhaps small mammals select plants with browning for girdling due to decreased presence of spines) is unclear. (3) Girdling is associated with greater natural and anthropogenic damage, including decapitation; plants that are damaged may be more attractive to rodents for girdling. Girdling is independent of presence of bird cavities and nurse architecture. (4) Lightning strike evidence was documented in far below 1% of the sampled plants, and fired-damaged plants also made-up less than 1% of the sampled plants. Decapitation made-up about 2% of the sample and most of those had little epidermal browning, but nearly 75% were girdled, compared to 45% girdling in the entire dataset. (5) Damage tends to increase with plant height. Even when height is controlled for, damage (including gunshot wounds) is associated with presence of bird cavities. Birds may select plants with entry wounds for cavity excavation, or perhaps some gunfire targets birds rather than plants. (6) Bird cavities are more strongly predicted by cactus height than number of branches, likely due to some disadvantages associated with branching (e.g., visibility, reduced exposure to winds that aid in cooling), as well as benefits of establishing higher on the plant (thus, necessarily, selecting taller plants for excavation sites) such as an elevated position above the ground and structural issues that may be associated with excavating smaller plants.

Columnar cacti are often keystone species (Fleming 2002), yet columnar cacti face a variety of pressures on their long-term survival. Epidermal browning is found across numerous taxa throughout the Western Hemisphere and is associated with early mortality (Evans and Fehling 1994; Evans et al. 1994b; Evans 2005). We show that it is also linked to presence of various types of damage in *Carnegiea*, including bird holes, girdling, and physical damage to the plant (e.g., gunshot wounds, proximal tree, fire).

In addition to the widespread (geographically and taxonomically) occurrence of epidermal browning, some columnar cactus species suffer from flat top decay syndrome and fatal bleaching, as well as human incursion and destruction (Bashan et al. 1995). It is imperative that we develop a global-scale understanding of the dynamics of these species and the factors that impact their survival and mortality.

ACKNOWLEDGMENTS

We thank the Arizona Army National Guard who own the data and granted us permission to analyze and publish our results from the dataset, and the Arizona Department of Game and Fish (AZGF) for providing useful background information and answering fieldwork and other related questions.

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